PLANT-BEARING COPROLITES FROM NORTH AMERICAN PENNSYLVANIAN COAL BALLS

by R. WILLIAM BAXENDALE

ABSTRACT. Well-preserved coprolites are described from North American Middle Pennsylvanian age coal balls. They are composed exclusively of plant material and are divided into three types on the basis of content and gross morphology. Type A are homogeneous in composition and average 4·5 × 2·5 × 1·9 mm in size. Type B coprolites are of heterogeneous composition, measure 6·5 × 3·5 × 3·1 mm, and are the most commonly occurring type. Type C coprolites, the least common type, are amorphous in composition and have an average size of 4·5 × 2·5 × 1·8 mm. Herbivores which may have produced the coprolites are discussed and it is concluded that they were probably deposited by fossil Arthropoda.

IN 1830 J. E. Dekay correctly interpreted the nature of coprolites from the Green Sand Formation (Cretaceous) of New Jersey. While today this interpretation is generally accepted (Häntzschel *et al.* 1968), early interpretations of coprolites were many and varied: 'cones of unknown vegetables' (Mantell 1822); 'petrified cones of fir' (Agassiz 1833); 'fossil urolites' (Duvernoy 1844); 'vomit balls' (Götzinger and Becker 1932); and 'eggs of undetermined origin' (Richter and Richter 1939).

Coprolites range in age from Ordovician (Richter and Richter 1939) into the Pleistocene (Light 1930) and Recent (Manning and Kumpff 1959). In size they range from less than 0·1 mm long to giant specimens of Cretaceous age up to 2 m long (Whitehouse 1934). An excellent review of the literature dealing with coprolites has been given by Amstutz (1958).

Although coprolites have been investigated for many years, the number of specimens composed of identifiable plant remains has remained small. Stoval and Strain (1936) described Tertiary faecal material in which plant fibres were replaced by chalcedony, quartz, and calcite. Jurassic coprolites composed mainly of caytonialean microsporophylls have been reported by Harris (1946, 1956, 1964), and Hill (1976) has reported similar material consisting of *Ptilophyllum* leaf fragments. Coprolites from borings in Carboniferous wood have been reported by C. Brongniart (1877) and Williamson (1880), while Scott (1977) has described coprolites from Carboniferous shales. Coprolites contained in coal balls were noted by Mamay and Yochelson (1953) and later figured by them as 'coprolitic pellets of unknown organism' (Mamay and Yochelson 1962, pl. 34, figs. 33, 34).

DESCRIPTION

Several hundred cellulose acetate peels from Middle Pennsylvanian North American coal balls were examined for coprolite content. The coal ball material represented collections from several localities in the midwestern United States. These localities included West Mineral and Cherokee in Kansas (Baxter and Hornbaker 1965); What Cheer, Lovilia, Oskaloosa, and Williamson in Iowa (Brotzman 1974); and Berryville in Illinois (Mamay and Yochelson 1962). From the peels initially examined, permanent microscope slide mounts were made of 170 coprolites, and these were examined at magnifications ranging from 2 × to 400 ×. All specimens are in the possession of the author.

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Most of the coprolites examined are oval when seen in longitudinal or oblique section. As reconstructed from serial sections, they can be shown to be of basically cylindrical form. In nearly longitudinal section, they appear elliptical and range in size from $1{\cdot}0 \times 0{\cdot}7$ mm to $14{\cdot}0 \times 5{\cdot}0$ mm, having average dimensions of about $5{\cdot}2 \times 2{\cdot}8$ mm. In transverse section, pellet diameters range from 0·5 to 8·0 mm with an average diameter of 2·5 mm. Due to the random orientation of coprolites within a coal ball, most initial saw cuts will yield oblique views of varying degree, rather like a random plane through the grass stalks in a haystack. Thus, as expected, only about 18% of the coprolites were seen in nearly transverse section and could be described as circular (circular here defined as the shorter diameter being at least nine-tenths of the longer), while the various oblique sections through the remainder explain some of the wide divergence of length and width.

An examination of the coprolite collection has shown the specimens to be readily divisible into three major categories, here designated as types A, B, and C. These types possess different characteristics of size and content and, in the limited sample of coal balls studied, are unequally distributed among several localities.

Type A coprolites

Type A coprolites can be described as homogeneous in that the plant fragments they contain can be assigned to a specific plant, a given tissue type, or a single genus and species. Such a type A coprolite is shown in Plate 65, fig. 1. It is composed exclusively of the epidermal and sarcotestal tissues of the cordaitean ovule *Nucellangium glabrum* Andrews (1949). The epidermis of *N. glabrum* is highly characteristic, being composed of thick-walled, radially elongated palisade-like cells that measure about 100 μm radially by 30 μm tangentially (Pl. 65, fig. 2). Sarcotestal cells are typically parenchymatous, usually with transverse section diameters of 85–160 μm. The coprolite tissue fragments agree closely with these measurements. For comparison, epidermal portions of an ovule of *N. glabrum* are shown in Plate 65, fig. 3.

EXPLANATION OF PLATE 65

Fig. 1. Type A coprolite composed exclusively of *Nucellangium glabrum* epidermis and sarcotesta fragments, × 4. KU983A; Oskaloosa, Iowa.

Fig. 2. Detail of *N. glabrum* epidermal fragments shown in fig. 1, × 163. KU983A; Oskaloosa, Iowa.

Fig. 3. Epidermis of a *N. glabrum* ovule, × 135. KU1005A; Oskaloosa, Iowa.

Fig. 4. Type A coprolite composed of *Alethopteris lesquereuxi* fragments, × 8. KU1463; West Mineral, Kansas.

Fig. 5. Pinnule of *A. lesquereuxi* in transverse section, × 10. KU1463; West Mineral, Kansas.

Fig. 6. Type A coprolites composed exclusively of *Florenites* microspores, × 32. KU56K; Berryville, Illinois.

Fig. 7. Single *Florenites* grain macerated from a type A microspore coprolite, × 150. KU480A; West Mineral, Kansas.

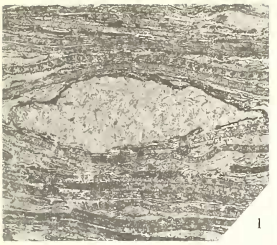
Fig. 8. Type B coprolite showing heterogeneous nature of contents, × 8. KU843; West Mineral, Kansas.

Fig. 9. Flat sheet of cordaitean(?) epidermal cells, × 64. KU19X; Lovilia, Iowa.

Fig. 10. Epidermal fragments in the form of curled strips, × 60. KU1018A; Oskaloosa, Iowa.

Fig. 11. Woody elements from a type B coprolite showing delicate scalariform thickenings, × 185. KU11C; Cherokee, Kansas.

Fig. 12. Tissue fragments strongly suggestive of annulus cells, × 120. KU10I; West Mineral, Kansas.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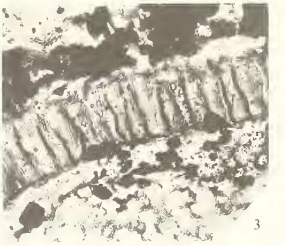
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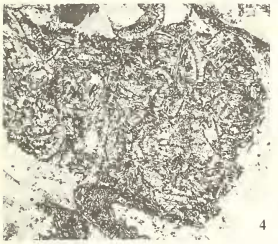
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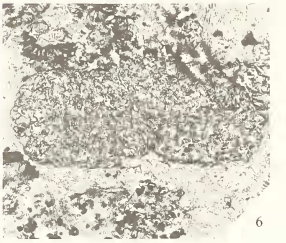
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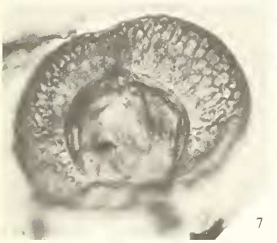
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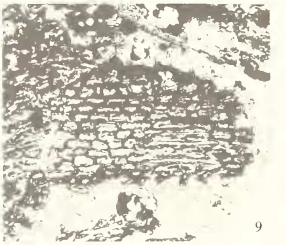
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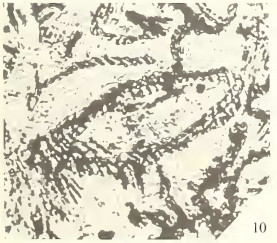
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Other type A coprolites contain only fragments of the pteridosperm pinnule *Alethopteris lesquereuxi* (Baxter and Willhite 1969), as shown in Plate 65, fig. 4. While both epidermal tissues and palisade cells may be present in a given coprolite, most conspicuous are the greatly enlarged cells of the hypodermis. These often measure 140 μm tangentially by 100 μm radially when seen in transverse section. The hypodermal tissue fragments contained in coprolites fit these dimensions very well. An *A. lesquereuxi* pinnule in transverse section is shown in Plate 65, fig. 5.

Readily visible in coal ball peels due to their distinctive pale yellow colour are type A coprolites composed entirely of compressed microspores (Pl. 65, fig. 6). Such coprolites are usually somewhat smaller than others assignable to type A, rarely exceeding 1·5 mm in diameter. Most are composed of spores and spore fragments of a single type, although a relative few (less than 10%) are composed of two or more spore types. The microspore coprolite shown in Plate 65, fig. 6, is typical of the majority, being composed exclusively of *Florenites* Schopf *et al.* (1944) grains and fragments. Coprolites of *Calamospora* Schopf *et al.* (1944) and individual grains of *Endosporites* Wilson and Coe (1940) were also observed. On maceration these coprolites often yield extremely well-preserved microspores (Pl. 65, fig. 7) as well as numerous corpus and saccus fragments.

Of the 170 specimens examined, sixty-seven, or about 40%, were classified as type A. In size they are somewhat smaller than the over-all average, usually measuring $4{\cdot}5 \times 2{\cdot}5 \times 1{\cdot}9$ mm. The relative proportion of coprolite types differs in the coal balls from different tips. Coal balls from Illinois localities seem to contain a high percentage of type A coprolites (84%) as compared to Kansas (27%) and Iowa (48%) localities.

Type B coprolites

Another eighty-four of the coprolites examined (50%) may be classified as type B (Pl. 65, fig. 8). Somewhat larger than type A specimens, type B coprolites have average dimensions of $6{\cdot}5 \times 3{\cdot}5 \times 3{\cdot}1$ mm. These coprolites are characteristic of coal balls derived from Kansas localities (64%), compared to Illinois (12%) and Iowa (35%) localities.

Type B coprolites are heterogeneous in content, being composed of tissue fragments apparently derived from several different plants or plant organs, and typically containing several types of tissue. Although the content is often extremely variable, fragments of epidermal tissue usually form a major component in most specimens. These epidermal remains may take the form of flat sheets (Pl. 65, fig. 9), the cells of which are very similar in size and shape to those of *Cordaites* leaves. Indifferently preserved stomata of the cordaitean type (Harms and Leisman 1961) may be present. Epidermal fragments may also occur as distinctively curled strips of tissue 40–50 μm wide and up to 900 μm in length (Pl. 65, fig. 10).

Often the bulk of a type B coprolite is composed of ragged, irregular masses of xylem tracheids and other woody elements. These tracheids may still show delicate spiral or scalariform wall thickenings (Pl. 65, fig. 11). Scraps of a tissue strongly suggestive of thick-walled annulus cells (Pl. 65, fig. 12) are frequently found intermingled with a wide variety of spores. These include the lycopsid megaspore *Sporangiostrobus* Bode (1928) and the sphenopsid *Calamospora* Schopf *et al.* (1944), as shown in Plate 66, figs. 1, 2.

Following their deposition, all faecal pellets must have been subject to invasion and decay by a wide range of organisms. Bradley (1946), for example, has described extraordinarily well-preserved silicified bacteria and fresh-water algae from a Wyoming coprolite of Eocene age. If a type B coprolite is of relatively loose organization, probable fungal remains may be seen between the component fragments. Aseptate fungal hyphae (Pl. 66, fig. 3) measuring about 10–15 μm in width are often present, as are circular, chytrid-like bodies (Pl. 66, fig. 4) with average diameters of 350–400 μm. Baxter (1975) has described similar forms of fossil fungi from American coal balls. Plate 66, fig. 5 shows what is interpreted as thick-walled fungal sclerotia. The sclerotia are from a type B coprolite, and are very similar in size and morphology to that illustrated by Cohen and Spackman (1977) from Recent Florida peat deposits; comparable structures are found in the ray cells of *Calamites* wood (Baxter, pers. comm. 1978). Cohen and Spackman (1977) suggest that the presence or absence of fungal remains is indicative of the relative dryness of the depositional environment and that the modern peat-forming habitats 'can be of great value in reconstructing environments of ancient coal swamps'.

Type C coprolites

A small percentage of the total coprolite collection (nineteen specimens or about 10%) represents a third distinctive form of fossil faecal material. Type C coprolites (Pl. 66, fig. 6) are characterized by the amorphous nature of their contents. Both in peel thin section and by maceration, plant remains in these coprolites are poorly preserved. These are tiny fragments of plant tissue with ill-preserved cell walls, and, while usually identifiable as being of botanical origin, such fragments rarely show sufficient anatomical detail to permit certain identification even of general tissue types. In addition, type C coprolites are often two-zoned, showing a well-defined rind and core, both with plant tissue fragments (Pl. 66, fig. 7). The rind of denser colour may be of considerable thickness and in some specimens accounts for nearly half of a radius. While a very thin rind portion may occasionally be present in both type A and type B coprolites, only in type C specimens is it typical and often massive.

In over-all size, type C coprolites are somewhat smaller than type B specimens, but have very similar dimensions to those of type A. An average type C specimen measures 4·5 × 2·5 × 1·8 mm. Coal ball material derived from sites in Iowa seems to show a higher percentage of this type of coprolite (16%) when compared with Illinois coal balls (4%) and Kansas material (9%). It is interesting to note that the distribution of type C coprolites is very uneven, often being seen as virtually the only type in a given coal ball. Rarely are type C coprolites found intermixed with types A and B.

Present to varying extents in the majority of coprolite specimens is a reddish-brown, resinous-appearing substance of unknown composition (Pl. 66, fig. 8). Being especially evident in type C specimens and those of relatively loose organization, this material may represent the petrified remains of mucus-like secretions from the lower digestive tract of the animal depositing the faecal material. Large quantities of such mucus could serve as a sort of glue, preserving and binding together the various faecal components into the characteristic shape of these coal ball coprolites.

In addition to the varieties of coprolites described above, groups of a few to several dozen very small spherical to slightly flattened pellets are very commonly encountered.

The dimensions of these small bodies are remarkably constant. One hundred specimens were measured and nearly 90% had diameters of 30–40 μm. The pellets often occur in loose aggregations, randomly arranged within the general mass of fragmentary plant debris. They are also found within certain plant tissues, often *Cordaites* leaves, where the pellets fill the mesophyll cavity (Pl. 66, fig. 9), or localized in the tissues of lepidodendroid leaf cushions (Pl. 66, fig. 10). Some specimens show a delicate rind, while in all, the preservation of constituent plant remains is extremely poor. These tiny coprolites do not appear to be restricted to any given coal ball locality but are equally distributed in all coal balls sampled.

DISCUSSION

While it is interesting to speculate on the nature of the Carboniferous herbivores that might have produced these coprolites, major difficulties arise when an attempt is made to assign them to any specific animal. As Hantzschel *et al.* (1968) point out, 'animals of very different systematic position may produce the same, or at least, very similar forms of coprolites'. This large array of potential producers can be somewhat narrowed, however, by the nature of the environment in which the coprolites were deposited as well as by the structure and contents of the pellets themselves.

Within any given coal ball, the orientation of coprolites relative to each other appears to be random, an indication that they were not significantly reworked by currents and that burial was fairly rapid (Hakes 1976). Small groups of faecal pellets deposited together seem to have remained in their original positions (Pl. 66, figs. 11, 12) much as described by Hill (1976). Such features as these would seem to indicate a low-energy depositional environment such as might have occurred in the shallow pools and low hummocks of a Carboniferous swamp-forest. The symmetrical, unflattened nature of the coal ball coprolites seems to indicate a pellet of sufficiently firm consistency to preserve the shape following burial.

The coal ball coprolites are composed exclusively of homogeneous or heterogeneous plant fragments, indicating a strictly herbivorous diet. It is a matter of

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EXPLANATION OF PLATE 66

Fig. 1. Somewhat distorted specimen of the lycopsid megaspore *Sporangiostrobus*, ×110. KU19Y; Lovilia, Iowa.

Fig. 2. Mass of microspores assignable to the sphenopsid genus *Calamospora*, ×350. KU19X; Lovilia, Iowa.

Fig. 3. Tangled mass of aseptate fungal hyphae, ×380. KU1414; West Mineral, Kansas.

Fig. 4. Circular, chytrid-like fungal(?) body, ×200. KU43K; West Mineral, Kansas.

Fig. 5. Thick-walled fungal sclerotia, ×300. KU1244; West Mineral, Kansas.

Fig. 6. Type C coprolite showing amorphous nature of contents, ×8. KU109; Oskaloosa, Iowa.

Fig. 7. Type C coprolite showing well-developed rind, ×11. KU1477; West Mineral, Kansas.

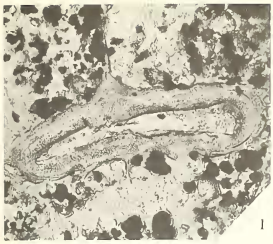
Fig. 8. Dark, resinous substance abundant in type C coprolites, ×10. KU108I; Oskaloosa, Iowa.

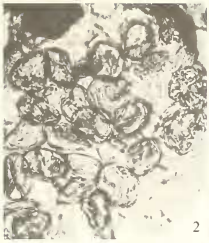
Fig. 9. *Cordaites* leaf with small coprolites filling the mesophyll cavity, ×58. KU581; Lovilia, Iowa.

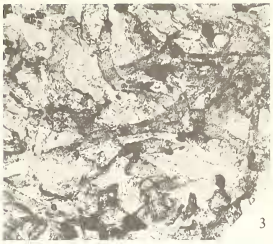
Fig. 10. *Lepidophloios* leaf cushion with small coprolites in parenchyma tissue, ×8. KU1175; West Mineral, Kansas.

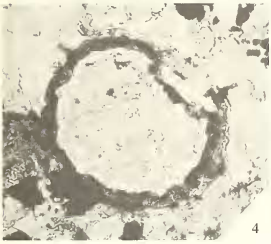
Fig. 11. Linear sequence of several sequentially produced coprolites, ×7. KU843C; West Mineral, Kansas.

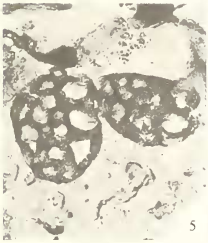
Fig. 12. Group of four coprolites showing undisturbed position, ×4. KU1231A; West Mineral, Kansas.

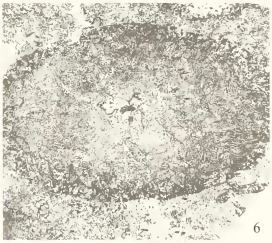


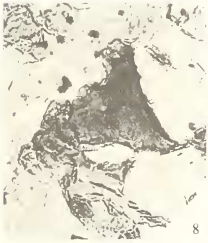


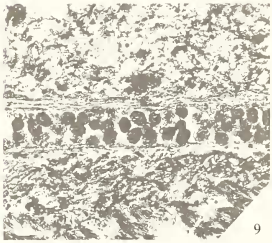


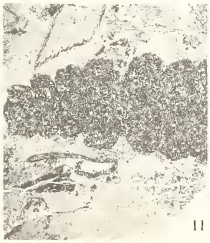


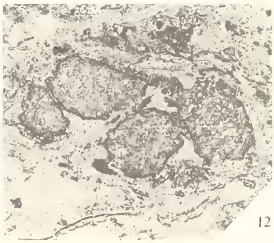












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speculation as to whether these herbivores consumed fresh vegetation, fallen and rotting plant matter, or possibly both. The presence of the three distinctive content types would seem to argue for the last possibility, however. Hill (1976) has suggested that the animal which produced his Yorkshire Jurassic specimens was 'perhaps the size of a sheep or large rabbit' and might have been reptile or mammal.

C. Brongniart (1877) has described and illustrated small globular coprolites from tunnels in fossil wood of probable Carboniferous age. He suggested that these pellets may have been produced by the insect '*Hylesinus*'; they are approximately the same size as the very small coal ball coprolites described above. Williamson (1880) investigated similar material from the British Carboniferous, finally concluding that the bodies 'were the copros of vegetable feeders [and that they] were invariably lodged in the cavities from which the tissues had been extracted'. The *Lepidophloios* leaf shown in Plate 66, fig. 10 seems to support this view since the parenchymatous tissue is well preserved except where it has been eaten away, the faecal pellets being deposited in the cavity thus produced. These tiny pellets are often found filling the mesophyll cavity of *Cordaites* leaves. Jacot (1939) has shown that conifer needles may be consumed internally by certain orabatid mites (Phthiracaridae) with no alteration of external leaf form, a situation very similar to that of the *Cordaites* leaf shown in Plate 66, fig. 9. Kevan (1968) compared droppings of modern orabatid mites with small pellets from a Carboniferous coal-seam nodule and concluded that the two were very similar. Kevan's comment that the faeces of some orabatid mites show very little undigested cellulose may be one reason that the tiny coal ball pellets described here show such consistently poor preservation of constituent plant fragments. Another possibility is that they may represent the excrement of an organism similar to a modern leaf miner (Crane, pers. comm. 1977); some or all of these pellets may merely represent stages in the degradation of cytoplasm and cell walls with the resemblance to pellets of faecal origin being only apparent.

Coprolites containing plant material from the Middle Coal Measures (Carboniferous) of Britain have been described recently by Scott (1977). He also suggests that such pellets might have been produced by phytophagous insects. Indeed, several members of the Arthropoda are especially attractive possibilities, since as Kevan *et al.* (1975) have pointed out, close interrelationships between arthropods and vascular plants have existed at least since Devonian times.

As noted by many researchers, a large and highly diverse insect fauna had become firmly established by the Upper Carboniferous. Tasch (1973) lists thirty-six orders of living and fossil insects, of which twelve orders are represented by the Upper Carboniferous and an additional ten by the end of Palaeozoic times. Insects of these several orders formed dense populations in the tropical swamp-forest habitats of the Carboniferous.

Hughes and Smart (1967) have listed as typical of the Carboniferous populations representatives of the orders Dictyoptera, Palaeodictyoptera, primitive Orthoptera, Ephemeroptera, Megasecoptera, and Odonata. Of these, the Megasecoptera and Odonata were carnivorous, presumably on other insects, and the feeding habits of the Ephemeroptera are uncertain. Species of cockroaches (Dictyoptera) however, were abundant, often making up 90% of the insects found in Carboniferous deposits (Carpenter 1940). Living in the litter layer, these insects were probably general and

indiscriminate feeders on the vast quantities of available vegetation. Scott (1977) has examined the faecal pellets of the extant cockroach *Blaberus*, and suggests that a somewhat smaller species might well produce faecal pellets of a size comparable to his Coal Measures compression specimens.

The Palaeodictyoptera are without living representatives, having a known geological range that extends only into the late Permian. Smart and Hughes (1972) make the intriguing suggestion that 'the proboscis of these Palaeodictyoptera . . . could have been used as a probe to work over the cones and capsules of the plants of that time for spores and pollen, and perhaps more especially for megaspores and the naked ovules of the seed ferns and early gymnosperms'. The analysis of coprolites from coal balls supports this possibility since both pollen (*Florenites*) and ovule fragments (*Nucellangium*) of the early gymnosperm *Cordaites* are abundantly represented. Primitive grasshopper and cricket forms (Orthoptera) may have fed by grazing on one or more levels of the swamp-forest floor and canopy, much as they do today.

Excluding members of the class Insecta, several other Carboniferous arthropods were probably of phytophagous habit. At least two major groups of the Myriapods are thought to have consumed plant material as at least a portion of their diets. Recent members of the class Diplopoda (millipedes) feed primarily on decaying plant matter and are frequently seen in rotting tree stumps. Dawson (1860, 1878) has described a fossil diplopod, *Xylobius sigillariae*, from a petrified stump of the arborescent lycopod *Sigillaria* in the Carboniferous of Nova Scotia.

Also within the Myriapoda, members of the extinct class Arthropleurida inhabited the late Carboniferous coal swamps and represent the largest terrestrial arthropod known. Adult specimens may have attained lengths of up to 6 ft (Rolfe 1969). Long thought to be carnivorous on the basis of a supposed cephalic limb, Rolfe and Ingham (1967) have shown *Arthropleura armata* to be incontrovertibly phytophagous. An investigation of a juvenile specimen showed the gut to be packed with vegetable debris, specifically 'carbonized wood tracheids with scalariform pitting [and] fragments of epidermis', apparently of lycopod affinity (Rolfe 1969). Such an animal as *Arthropleura*, depending on size and age, could well have produced faecal pellets as large or larger, and of similar composition to the coprolites described from coal balls.

A point almost inevitably mentioned by researchers working on coprolitic material is the usual near-total absence of other animal traces. In the vast majority of cases, no animal remains of any sort are associated with the faecal pellets in a manner suggestive of an association between them. Unfortunately the situation is the same for coprolites contained in coal balls. No animal remains that even vaguely suggest terrestrial arthropods are found in coal balls, let alone in direct association with the coprolites. This feature is hard to explain in light of the famous Mazon Creek fauna of the same geological age (Middle Pennsylvanian) and geographical location (Illinois) as some of the coal balls described here, where over 100 species of insects, and numerous species of plants, have been reported from the ferruginous nodular concretions in coal strip mines (Richardson 1956). Hughes and Smart (1967) suggest that 'The fossil record of insects is very discontinuous because the nature of their bodies is such that they will only be fossilized under particularly favourable circumstances', and later go on to note that 'it seems that the conditions of sedimentation that have to occur if

insect remains are to be preserved and not ground to unrecognizable fragments, are rare' (Smart and Hughes 1972). The mechanism behind the formation of coal balls is poorly understood and highly controversial. Thus it must be assumed that somehow the specific depositional conditions necessary for the preservation of recognizable insect fragments did not occur, even though structures as delicate as pollen grains with nuclei (Baxter 1950) and fungal clamp connections (Dennis 1970) were preserved.

CONCLUSIONS

The abundance of plant-containing coprolites in coal balls provides additional evidence of a large and diverse population of phytophagous organisms during Carboniferous times. Coprolites provide a means of studying the dietary intake of these herbivores, providing an insight into the composition of contemporary plant communities, while at the same time supplying information on the probable size of the producers and the nature of the environment in which they lived. Several groups of arthropods may have been possible producers of the coal ball coprolites, including various members of the Dictyoptera (cockroaches), Palaeodictyoptera, Orthoptera (grasshoppers and crickets), Diplopoda (millipedes), and Arthropleurida.

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R. WILLIAM BAXENDALE

Department of Botany and Microbiology
Arizona State University
Tempe
Arizona 85281
U.S.A.

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